

TWO NEW BAJOCIAN MICROCONCH OTOITID AMMONITES AND THEIR SIGNIFICANCE

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ABSTRACT. Two new Bajocian (Middle Jurassic), microconch species belonging to the ammonite family Otoitidae, *Trilobiticerias* (*Trilobiticerias*) *cricki* nov. and *Emileia* (*Otoites*) *douvillei* nov., are described, and are paired with their probable macroconch partners, *T. (Emileites)* *malenotatus* (Buckman) and *E. (E.) subcadiconica* Buckman respectively. The stratigraphic distribution of the main members of the subfamily Otoitinae in southern England shows that the two new species fill an important gap in our knowledge of this subfamily. In particular *T. (T.) cricki* is of fundamental importance, as it is the undoubted ancestor to both *Emileia* and *Frogdenites* and possibly also *Pseudotoites*. With their restricted stratigraphic range and wide geographic distribution, these new species are valuable stratigraphic indices for delimiting the base of the *ovalis* Subzone of the *laeviuscula* Zone. The most important exposures of the *ovalis* Subzone are discussed and the famous fauna described from the south of France by Douville is revised.

DURING the course of a recent stratigraphic study of the Bajocian rocks (Middle Jurassic) of southern England (Parsons 1974, pp. 164–171), large ammonite collections have been made from some long-neglected horizons. In particular the *ovalis*, or so called ‘Lower white iron-shot’ bed of Dundry Hill, near Bristol (Buckman and Wilson 1896, pp. 708–709, table iv), has yielded an interesting assemblage, which may be correlated with the *ovalis* Subzone of the *laeviuscula* Zone (Parsons 1974, p. 169)—see Table 1 for the zonal scheme used here. The majority of ammonites

TABLE 1. Zones and relevant subzones of the Lower Bajocian substage (= Middle Bajocian *sensu* Arkell 1956), after Parsons 1974.

	ZONES	SUBZONES
LOWER BAJOCIAN	<i>Stephanoceras humphriesianum</i>	
	<i>Emileia (Otoites) sauzei</i>	
	<i>Witchellia (Witchellia) laeviuscula</i>	<i>W. (W.) laeviuscula</i>
	<i>Hyperhoceras discites</i>	<i>Sonninia ovalis</i>

collected from this horizon (+56%), belong to the *Witchellia*/*Pelekodites* dimorphic group. However, intensive collecting revealed that a small proportion of the total fauna consists of two, as yet undescribed, species belonging to the microconch subgenera *Otoites* and *Trilobiticerias*. A study of the previous literature and pre-existing museum collections showed that these stratigraphically important species had been collected and recognized as distinct for some considerable time; it has merely taken a hundred years for them to be formally described. The small physical size of these two new microconch species, as well as their relative rarity in comparison with the abundant *Witchellia*, goes some way towards explaining their absence in previous works on the Bajocian Otoitidae (Westermann 1954).

As already noted, these two new species form only a minor part of the total ammonite fauna of this age in England. However, at comparable horizons in southern Europe the sonninid ammonites are less dominant, whilst the stephanoceratids are relatively more abundant. It is thus not surprising that this area of Europe has produced the majority of previous records of these two new species, particularly the south of France, Portugal, and Sicily. With their wide geographic distribution and relatively restricted stratigraphic range, these ammonites are of great value for correlation purposes, particularly for between sonninid-dominated north-west Europe and the Tethyan region. These taxa are also of considerable phylogenetic importance, as they form a critical link between the early stephanoceratids of the *concavum/discites* Zones and the more abundant forms of the upper *laeviuscula/sauzei* Zones. As *Emileia* (*Otoites*) *douvillei* nov. and *Trilobiticeras* (*Trilobiticeras*) *cricki* nov. are characteristic of the *ovalis* Subzone of the *laeviuscula* Zone, some discussion of the stratigraphy of this horizon in southern England and elsewhere in Europe is given.

Numbers preceded by these abbreviations refer to ammonites in the following collections:

BMNH.	The British Museum (N.H.), London.
Cb.	Bristol City Museum.
IGS.	The Institute of Geological Sciences, London.
M.	The École des Mines Collection, Université de Paris-Sud, Paris.
OUM.	The Oxford University Museum.
SM.	The Sedgwick Museum, Cambridge.
CP.	The author's collection, Liverpool University.

Under type species M = macroconch and m = microconch.

SYSTEMATIC DESCRIPTIONS

Class CEPHALOPODA

Subclass AMMONOIDEA

Superfamily STEPHANOCERATACEA Neumayr, 1875

Family OTOITIDAE Mascke, 1907

The classification of the Otoitidae follows Westermann (1964), who divided this family between two subfamilies, the Otoitinae and Sphaeroceratinae.

Subfamily OTOITINAE Mascke, 1907

The generic classification within this subfamily follows Westermann (1964, pp. 51–54), except for the inclusion of *Frogdenites*, which on both morphological and stratigraphic criteria has been transferred from the Sphaeroceratinae.

Genus *Emileia* Buckman, 1898

Type species. Emileia (*Emileia*) *brocchii* (J. Sowerby, 1818), (M.).

Diagnosis. A group of macroconch and microconch, sphaeroconic ammonites, which on the inner whorls bear 'club'-shaped primary ribs, terminated by blunt nodes, from which divide two or more rounded secondary ribs. The nominate subgenus consists of medium to large-sized macroconch ammonites, with a terminal constriction and flared-mouth border, and which vary from involute sphaerocones via cadicones to evolute platycones.

Subgenus *Otoites* Mascke, 1907

Type species. Emileia (Otoites) sauzei (d'Orbigny, 1846), (m.).

Diagnosis. A group of moderately small sized, lappeted microconch ammonites, which are characteristically involute sphaerocones, with a pronounced contraction of the body chamber. The ribbing style on the inner whorls is identical to its macroconch, *Emileia s. str.*, that is 'club'-shaped primary ribs, dividing into three to four finer secondaries. On its outer whorls, *Otoites* tends to develop sharp tubercles or spines at this point of division, whilst on the body chamber the secondary ribs tend to become inflated and coarsened, often with an alternation of strength on the last half whorl, with every second, third, or fourth rib being more inflated than its neighbour.

Emileia (Otoites) douvillei sp. nov.

Plate 17, figs. 6, 7, and 9; text-fig. 1

- 1885 *Sphaeroceras sauzei* d'Orbigny; Douvillé *non* d'Orbigny, p. 41, pl. III, fig. 9a-b.
 ?1921 *Otoites sauzei*; Riche and Roman *non* d'Orbigny, p. 138, pl. 6, fig. 8.
 1925 *Sphaeroceras (Otoites) sauzei* d'Orbigny; Renz *non* d'Orbigny, p. 32, pl. II, fig. 8 and 8a.
 ?1929 *Emileia sauzei* d'Orbigny; Lanquine *non* d'Orbigny, p. 293, pl. ix, fig. 6.
 1960 *Otoites* sp. (*O. sauzei* Roman *non* d'Orbigny); Lelièvre, p. 17.
 1960 *Otoites* sp.; Dubar, p. 52, pl. vii, figs. 25-26 and ?24.
 1961 *Otoites cf. sauzei* (d'Orbigny) (Douvillé, 1885, pl. 3, fig. 9); Ruget-Perrot, p. 54.
 ?1967 *Otoites* sp.; Gabilly and Rioult, p. 3.
 ?1974 *Emileia (Otoites)* sp. nov.; Parsons, p. 168.
 ?1975 *Emileia (Otoites)* sp. nov.; Morton, pp. 84-85, pl. 16, figs. 5-6.
non 1954 *Otoites fortis* n. sp.; Westermann, pp. 103-106, pl. 3, figs. 2-4; text-figs. 10 and 21.

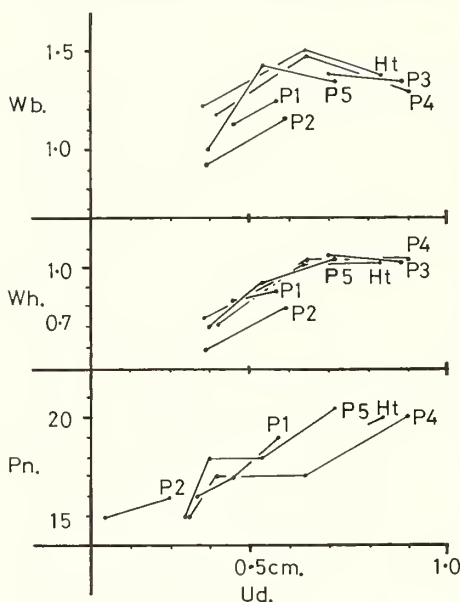
Material. Two specimens — 0.30 m from the top of bed 2, Barns Batch Spinney (National Grid Reference ST 557 659), Dundry Hill, Bristol (Buckman and Wilson 1896, p. 689), BMNH. C79428-79429; five Dundry specimens from old museum collections, BMNH. C75242, IGS. 25189, Cb. 4744, Cb. 4957-4958, and one specimen + 0.30 m from the base of bed 4, Bruton Railway quarry (ST 682 345), Bruton, Somerset (Richardson 1916, p. 495), BMNH. C79432, a total of eight specimens.

Dimensions. Holotype, Cb. 4744, from Dundry Hill, and by matrix from the *ovalis* bed. It is complete, with the base of lappets, and just over three-quarters of a whorl of body chamber at a maximum diameter of 2.67 cm.

Diameter (D)	Umbilical diameter (Ud)	Number of primary ribs (Pn)	Whorl height (Wh)	Whorl breadth (Wb)	$\frac{Wb}{Wh}$
2.50	0.83 (33%)	c. 20	1.04 (42)	1.36 (54)	1.31
2.16	0.64 (30)	—	1.01 (47)	1.50 (69)	1.49
First paratype, BMNH. C79429, with a quarter whorl of body chamber.					
1.96	0.57 (29)	19	0.89 (45)	1.25 (64)	1.4
1.7	0.46 (27)	17	0.84 (49)	1.13 (67)	1.35
Second paratype, BMNH. C79428.					
1.7	0.59 (35)	—	0.8 (47)	1.15 (68)	1.44
1.31	0.39 (30)	—	0.6 (46)	0.92 (70)	1.53

Description. A small (c. 2.3-2.7 cm diameter), sphaeroconic ammonite, with a strongly contracted body chamber, which extends for three-quarters to one whorl. The prorsiradiate primary ribs are short, blunt, and expand into 'club'-shaped nodes at

the point of division into three to four secondary ribs. These secondaries are relatively coarse, rounded rather than sharp, and bend forward only slightly over the rounded venter. The primary ribs weaken on the body chamber, whilst the secondaries, particularly on the last quarter whorl, are reduced to two per primary, and become



TEXT-FIG. 1. A plot of whorl breadth (Wb), whorl height (Wh), and number of primary ribs (Pn), against umbilical diameter (Ud), for *Emileia (Otoites) douvillei* sp. nov. Ht = holotype; P = paratype.

inflated and coarsened, often with a tendency to become irregularly swollen. Thus on the last half whorl of the third paratype (IGS. 25189), every second or third rib is more expanded than its neighbour. The relative primary rib density increases rapidly (see text-fig. 1), from 15 to 16 per whorl on the inner whorls, to 20 to 21 on the body chamber. There is very little relative change in whorl cross-section, which stays more or less rounded, but depressed throughout ontogeny. The exception to this is found on the last quarter whorl of the body chamber, where, associated with the rapid uncoiling of the umbilical seam, there is a marked decline in whorl breadth (Wb), relative to whorl height (Wh)—see text-fig. 1. This rapid uncoiling of the body chamber changes the shell shape from a slightly sphaeroconic, to a more evolute form, although it is never as evolute as *Trilobiticerat* (*T.*) *cricki* nov. The mouth border is characterized by a pair of spatulate lappets, which extend from the mid-whorl position (see Pl. 17, fig. 6a).

Type series (six specimens). The holotype (Pl. 17, fig. 6a–b), the best-preserved British

specimen, comes from an old collection in the Bristol City Museum (Cb. 4744). The matrix of this specimen is identical to that of bed 2, Barns Batch Spinney, Dundry (Buckman and Wilson 1896, p. 689); that is, the *ovalis* bed, which is unique to the west side of Dundry Hill. The first paratype (BMNH. C79429), has only a quarter whorl of body chamber, but it is clearly very similar to the holotype in both proportions and ornament (see Pl. 17, fig. 9a–b), and like the second paratype (BMNH. C79428), it was collected *in situ* from bed 2, Barns Batch Spinney, Dundry, thus confirming the type horizon of the holotype. The third paratype (IGS. 25189), has the best-preserved lappets, whilst the fourth is a well-preserved specimen (Cb. 4957), which is recorded on its label as coming from the 'Sherborne district' of north Dorset. However, the matrix of this specimen, which is totally atypical of the Sherborne area, would suggest a true provenance from the *ovalis* bed of Dundry. Lastly the fifth paratype (BMNH. C75242), is another well-preserved specimen, with a matrix characteristic of the *ovalis* bed (Pl. 17, fig. 7a–b).

Sexual dimorphism. Sexual dimorphism is well marked in this group. *Emileia (Otoites) douvillei* nov., like other members of this subgenus, shows typical microconch

features. The mature shell is of relatively small size, and exhibits well-developed lappets. The corresponding macroconch is less well represented in the *ovalis* bed. A typical specimen from Dundry, *ex* Etheridge Collection, BMNH. C75279, is an involute, slightly cadiconic form, with bullate primary ribs and a quarter of a whorl of body chamber at a diameter of 4.1 cm, see Plate 17, fig. 8. The matrix of this specimen suggests the *ovalis* bed as its source. This is confirmed by the occurrence of a complete specimen, with a plain mouth band, 9.0 cm in diameter, from the *ovalis* bed of West Dundry (Bristol University, Department of Geology, No. 67). These macroconchs are best referred to *E. (E.) subcadiconica* S. Buckman (1927, in 1909–1930, pl. 711). The type specimen of the latter (IGS. 49304), although fragmentary and wholly septate, exhibits, as noticed by Buckman (*loc. cit.*), a typical *ovalis* bed matrix.

Stratigraphic range. *E. (O.) douvillei* appears to be characteristic of the *ovalis* Subzone of the *laeviuscula* Zone. However, this taxon probably ranges up into the base of the *laeviuscula* subzone, although the specimens referred to it from the basal part of the 'Sandford Lane fossil bed', near Sherborne, Dorset (ST 628 179), are possibly not conspecific. The latter are slightly larger, with a different primary rib density (= *Otoites* sp. nov.; Parsons 1974, p. 168). By way of comparison, a single specimen from this locality and horizon, in the Reed Collection of the Yorkshire Museum is figured here (Pl. 17, fig. 4).

Geographic range. Apart from Dundry Hill, and more doubtfully Sandford Lane, the only other British localities to yield this species are Bruton Railway quarry, Bruton, near Castle Cary, Somerset (Richardson 1916, p. 495, bed 4), which has yielded one specimen, BMNH. C79432, and possibly Berreraig Burn, Isle of Skye, Scotland (= *Otoites* sp. nov.; Morton 1975, pl. 16, figs. 5 and 6). It is impossible to be certain of the latter, as the specimen is not well preserved and is badly localized. Elsewhere this species has been recorded from the south of France (Douville 1885; Lanquine 1929), Sicily (Renz 1925), Portugal (Ruget-Perrot 1961), and Morocco (Dubar 1960).

Discussion. As may be seen from the synonymy list, the presence of this species has been noted by numerous authors, most of whom commented on its distinctive nature. This species has been named in honour of H. Douville, who was the first to figure it (Douville 1885). Dubar (1960, p. 52) has given the most detailed previous description of this taxon, and he also pointed out the differences between his specimens and the other species of *Otoites* which had been figured up to that time. The criteria separating *E. (O.) douvillei* from *E. (O.) fortis* (Westermann), with which it has been equated (Westermann 1954, p. 103), were given by Dubar (1960) as: its small size, being half to one-third of that of other *Otoitids*, the very strong contraction of its body chamber, and the modification of its ornament near the mouth border, particularly the loss of tubercles or nodes on the last two ribs. These characters appear perfectly valid, although there is some variation in the amount of contraction of the body chamber, since not all specimens show this to the same degree, notably those figured by Douville (1885, pl. III, fig. 9) and Lanquine (1929, pl. ix, fig. 6). It is also interesting to note Dubar's comment (*op. cit.*, p. 52) 'The exact age of this small form is still to be established . . . perhaps this *Otoites* will be the most ancient';

as it can now be shown that this species is indeed the oldest yet recorded belonging to the subgenus *Otoites*.

There are really no other species of *Otoites* closely related to *E. (O.) douvillei*, since they are all of much larger size and occur at higher stratigraphic horizons. In fact the most closely related forms are the more inflated variants of *T. (T.) cricki* nov. which are found together at the same horizon. These two groups are very much alike in size and relative proportions, the main difference being in the style of ribbing. It is thus reasonable to suggest that *E. (E.)/(E.) Otoites* evolved from the *T. (T.)/T. (Emileites)* group at the base of the *laeviuscula* Zone, especially since no specimens of either *Otoites* or *Emileia* have been found below this horizon.

Genus *Trilobiticeras* Buckman, 1919

Type species. Trilobiticeras (Trilobiticeras) trilobitoides Buckman, 1919 (m.).

Subgenus *Trilobiticeras* Buckman, 1919

Diagnosis. A group of very small-sized microconch ammonites, with coronate inner whorls. It has sharp primary ribs, which are terminated by sharp tubercles or spines at the point of division into the fine secondary ribs. The secondaries, of which there are three to five per primary, sweep forward over an arched venter. The body chamber shows an uncoiling of the umbilical seam, a coarsening of the tubercles and secondary ribs, a fading of the primary ribs, and it is terminated by a well-differentiated mouth border, with two spatulate lappets. The stratigraphic range of the subgenus is the same as that of *Emileites*, its macroconch counterpart, that is, upper *concauum* Zone to middle *laeviuscula* Zone.

Trilobiticeras (Trilobiticeras) cricki sp. nov.

Plate 17, figs. 1-3 and 5; text-fig. 2

1885 *Sphaeroceras sauzei* (variété ?); Douvillé non d'Orbigny, p. 41, pl. III, fig. 10.

1894 *Sphaeroceras* sp. nov.; Crick, p. 436.

1972 *Trilobiticeras trilobitoides* Buckman; Galacz non Buckman, pp. 43-44, text-fig. 2a-d.

1974 *Trilobiticeras* sp. nov.; Parsons, p. 169.

EXPLANATION OF PLATE 17

(All specimens are coated with ammonium chloride.)

Fig. 1a-b. *Trilobiticeras (Trilobiticeras) cricki* nov. (m.), holotype, BMNH. C79426, *in situ* bed 2, Barns Batch Spinney (Buckman and Wilson 1896), Dundry Hill, Bristol; $\times 1.5$.

Fig. 2a-b. *T. (T.) cricki* nov., first paratype, BMNH. C79427, *in situ* bed 2, Barns Batch Spinney; $\times 1.5$.

Fig. 3a-b. *T. (T.) cricki* nov., third paratype, BMNH. C75287, Dundry; $\times 1.5$.

Fig. 4. *Emileia (Otoites)* sp. cf. *E. (O.) douvillei* nov. (m.), Reed Collection, Yorkshire Museum, YM. 989, the 'fossil-bed', Sandford Lane, Dorset; $\times 1.0$.

Fig. 5. *T. (T.) cricki* nov., second paratype, BMNH. C79425, *in situ* bed 2, Barns Batch Spinney; $\times 1.5$.

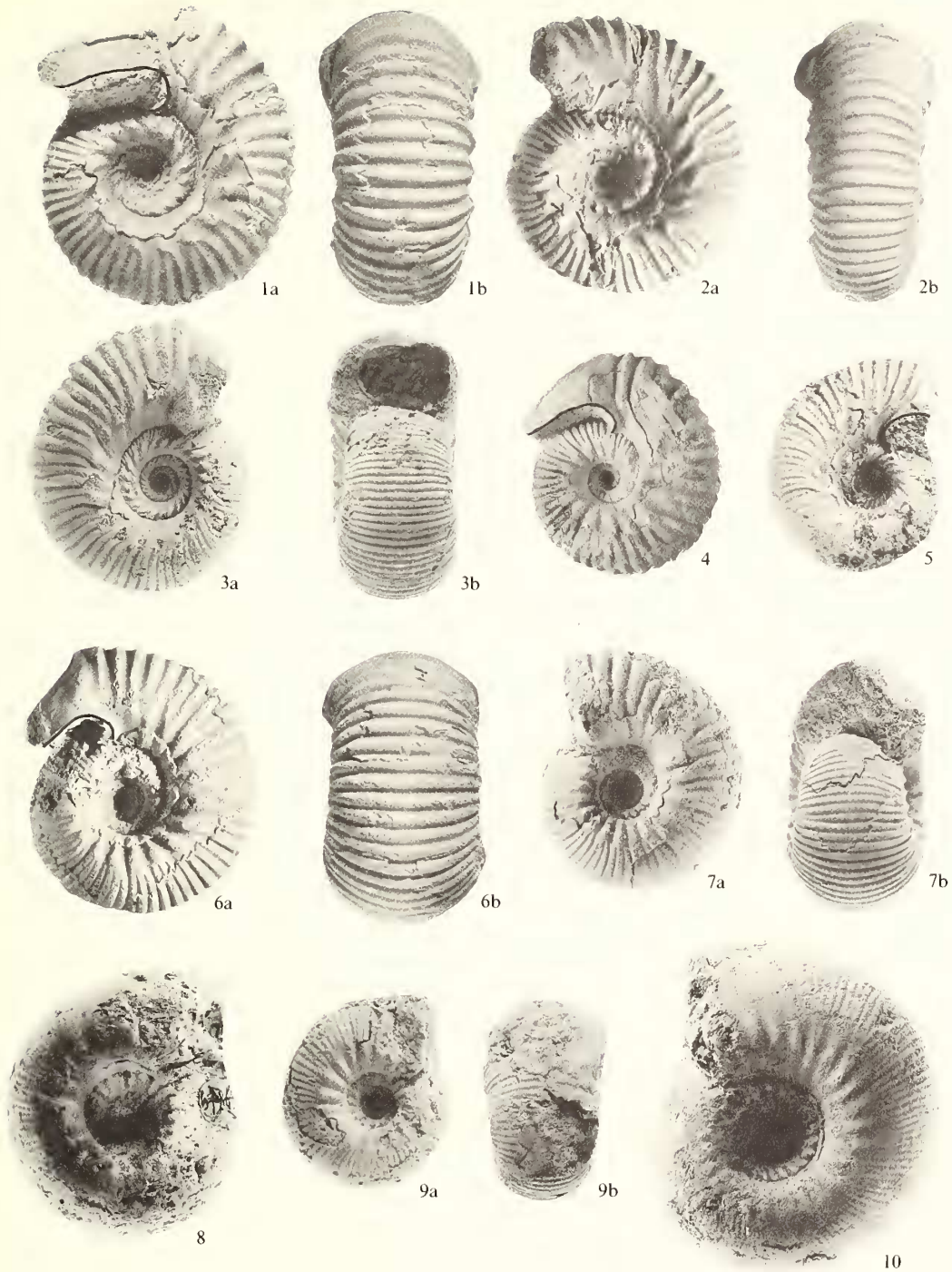
Fig. 6a-b. *E. (O.) douvillei* nov. (m.), holotype, Cb. 4744, Dundry; $\times 1.5$.

Fig. 7a-b. *E. (O.) douvillei* nov., fifth paratype, BMNH. C75242; $\times 1.5$.

Fig. 8. *E. (Emileia) subcadiconica* S. Buckman (M.), BMNH. C75279, Dundry; $\times 1.0$.

Fig. 9a-b. *E. (O.) douvillei* nov., first paratype, BMNH. C79429, *in situ* bed 2, Barns Batch Spinney; $\times 1.5$.

Fig. 10. *T. (Emileites) malenotatus* (S. Buckman) (M.), BMNH. C73979, Dundry; $\times 1.0$.



PARSONS, Bajocian otoitid ammonites

Material. Three specimens from the top 10 cm of bed 2, Barns Batch Spinney, Dundry Hill, Bristol, BMNH. C79425–79427; one specimen from bed 4b, Seavington-St.-Mary (ST 398 144), Somerset (Parsons and Torrens in Torrens 1969, p. A27), BMNH. C79433; one specimen from bed 6, Bruton Railway quarry, Bruton, Somerset, BMNH. C79431; one specimen from the base of the 'fossil-bed', Sandford Lane, Sherborne, Dorset (Buckman 1893, p. 492, bed 6), BMNH. C79430; one specimen from Cape Mondego, Portugal (Ruget-Perrot 1961, p. 27, bed 5), BMNH. C79435; one specimen from Bradford Abbas, near Sherborne, Dorset, SM. J24550; and three Dundry specimens from old museum collections, BMNH. C75270, C75287, and OUM. J1163. A total of eleven specimens, plus numerous (+100) other less well-localized specimens in various old museum collections.

Dimensions. Holotype, BMNH. C79426, a complete specimen, with lappets and three-quarters of a whorl of body chamber.

D	Ud	Pn	Wh	Wb	Wb Wh
2.82	0.96 (34%)	17	1.19 (42)	1.36 (48)	1.14
2.23	0.75 (34)	16	1.0 (45)	1.32 (59)	1.32

First paratype, BMNH. C79427, a complete specimen, with lappets and three-quarters of a whorl of body chamber.

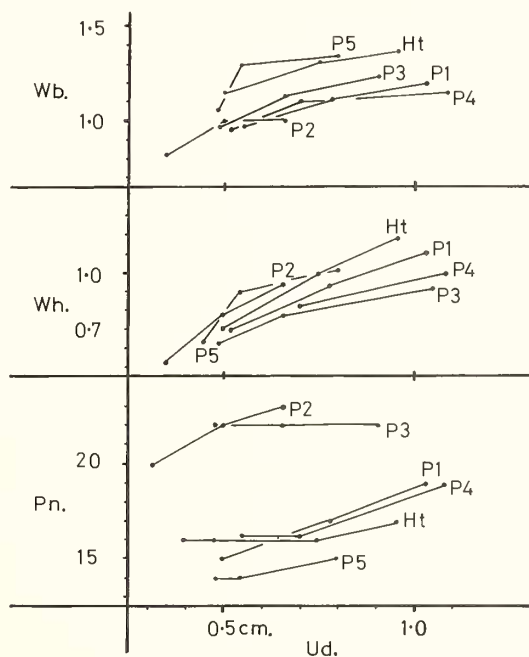
2.85	1.03 (36)	19	1.11 (39)	1.2 (42)	1.08
2.2	0.78 (36)	17	0.94 (43)	1.11 (51)	1.18

Second paratype, BMNH. C79425, a complete specimen, with lappets and three-quarters of a whorl of body chamber.

2.14	0.66 (31)	23	0.95 (44)	1.0 (47)	1.05
1.65	0.50 (30)	22	0.78 (47)	1.0 (61)	1.28

Description. A small microconch ammonite (maximum diameter, modal value from ninety-five specimens = 2.65 cm), with cadicone inner whorls and a rapid contraction of the body chamber, which extends for three-quarters of a whorl. The primary ribs are sharp, prorsiradiate, and approximately one-third of the length of the secondaries. The secondary ribs are extremely fine on the inner whorls, where there are three to five per primary, whilst on the outer whorls, where there are only two to three per primary, they are coarser and more widely spaced. The fine, sharp tubercles at the point of division of the secondary ribs, become stronger on the body chamber, whilst the primary ribs weaken, and in some cases become virtually obsolescent. The primary rib density is fairly constant on the inner whorls, but shows a marked increase on the penultimate and last whorls, see text-fig. 2. This rib density varies from individual to individual, between 14 and 23 ribs per whorl, the majority of specimens having in the region of 17 to 18 on the last whorl. The contraction of the body chamber results in a relative reduction in whorl breadth, as is clearly shown in text-fig. 2. Since the whorl height continues to increase, although at a reduced rate, right up to the mouth border, there is a pronounced change in the whorl cross-section; the cadicone inner whorls, with an arched venter ($Wb/Wh = 1.32$), take on a more rounded cross-section ($Wb/Wh = 1.14$). The mouth border is characterized by fine spatulate lappets, which develop in the mid-whorl position, see Plate 17, fig. 1a, and which are usually preceded by a more coarse and prominent secondary rib. Although the inner whorls are cadicone, the contraction of the body chamber gives a more planulate appearance to the mature shell, which is one of the more evolute ootitid microconchs ($Ud/D \times 100 = 30\text{--}40\%$). The suture line is difficult to make out on most specimens, but it appears similar to that of the Hungarian specimen (Galacz 1972, fig. 2).

Type series (the six well-localized specimens). The holotype (BMNH. C79426), is one of the dominant morphotypes (Pl. 17, fig. 1*a-b*), whilst the first paratype (BMNH. C79427) is a slightly less inflated and more finely ribbed variant (Pl. 17, fig. 2*a-b*). The second paratype (BMNH. C79425), is a small, even more finely ribbed form (Pl. 17, fig. 5). All three of the above specimens were collected *in situ* from bed 2 (top 10 cm), Barns Batch Spinney, Dundry Hill. The third paratype from Dundry (BMNH. C75287, *ex* Charlesworth Coll.), is a large fine ribbed specimen (Pl. 17, fig. 3*a-b*), whilst the fourth (BMNH. C75270, *ex* Pratt Coll.) is one of the more evolute forms. Finally the fifth paratype (OUM. J1163, *ex* Goddard Coll.), also from Dundry, is the most coarsely ribbed form I have seen; at a diameter of 2.4 cm, with more than two-thirds of a whorl of body chamber, it has fifteen primary ribs, at an umbilical diameter of 0.8 cm (33%).



TEXT-FIG. 2. A plot of whorl breadth (Wb), whorl height (Wh), and number of primary ribs (Pn), against umbilical diameter (Ud), for *Trilobiticerases* (*Trilobiticerases*) *cricki* sp. nov. Ht = holotype; P = paratype.

Sexual dimorphism. This group has well-marked sexual dimorphism and *Trilobiticerases* (*T.*) *cricki* nov. exhibits typical microconch features: small size, with well-developed lappets. The corresponding macroconch, although not quite as abundant as its partner, is well represented in the *ovalis* bed at Dundry. These specimens are identical in shell form, style of ribbing, and general ornament, to all but the last whorl of *T.* (*T.*) *cricki* nov., but differ by still being wholly septate at a diameter in

excess of that attained by mature specimens of the latter. A typical *ovalis* bed macroconch specimen from Dundry (BMNH. C73979) is figured here (Pl. 17, fig. 10). This has one whorl of body chamber at a diameter of 5.05 cm. There are two specific names available for this group. The type specimen of *T. (Emileites) malenotatus* (Buckman 1927, in 1909-1930, pl. 702, IGS. 49293), although rather fragmentary and poorly localized, is undoubtedly very similar to many of these macroconchs. As noted by Buckman (loc. cit.), the matrix of this specimen is typical of the *ovalis* bed of Dundry. The type specimens of *T. (E.) liebi* (Maubeuge 1955, pl. 9, figs. 1a-d and 2) are even closer in gross morphology to the Dundry forms, and it is likely that this species is a subjective junior synonym of *T. (E.) malenotatus*.

Stratigraphic range. The majority of members of this species have come from the *ovalis* bed of Dundry, which is *ovalis* Subzone, *laevinscula* Zone in age (Parsons 1974, p. 169). The lowest occurrence of this species appears to be the *discites* Zone. A single specimen from Bradford Abbas, near Sherborne, Dorset (SM. J24550), has the 'iron-shot', black-stained matrix typical of the top part of the Bradford Abbas 'fossil-bed', which is of this age (Parsons 1974, p. 170). A few specimens have been found as high as the *laevinscula* Subzone of the *laevinscula* Zone at Sandford Lane quarry, Sherborne (BMNH. C79430; Buckman 1893, p. 492, bed 6c) and at the South Main-road quarry (ST 567655), Dundry (CP. 2403; Buckman and Wilson 1896, p. 691, bed 5).

Geographic range. Outside of the localities in southern England mentioned above, this species has been figured from Hungary (Galacz 1972, fig. 2) and south-east France (Douvillé 1885, pl. III, fig. 10; M.121), whilst I have collected it from Cape Mondego, Portugal (BMNH. C79435; Ruget-Perrot 1961, p. 27, bed 5).

Discussion. This species is named in honour of G. C. Crick, who first noticed its presence in the Inferior Oolite of Dundry Hill (Crick 1894, p. 436). *T. (T.) cricki* nov. is closest in gross morphology to specimens from the upper *concauum*/lower *discites* Zones of southern England, which have been included in *T. (T.) punctum* (Vacek); (Westermann 1964, pl. 6, figs. 5-6). It is difficult to establish if the small, fragmentary type specimen of this latter species (ibid., pl. 6, fig. 7a-b) is truly conspecific with the larger specimens figured by Westermann (loc. cit.), from Seavington-St.-Mary, Somerset. If it is, then this group is consistently more inflated, with a more depressed and coronate whorl section than *T. (T.) cricki*. These two also have distinct stratigraphic distributions at Seavington-St.-Mary. The more inflated forms, *T. (T.) punctum*, are relatively common in bed 3 (Parsons and Torrens in Torrens 1969, p. A27), which is upper *concauum* Zone in age, whilst the specimen of *T. (T.) cricki* (BMNH. C79433), came from a higher horizon, bed 4b, which is *ovalis* subzone in age. However, the possibility must remain that the lectotype of *T. (T.) punctum* is nothing but the poorly preserved inner whorls of a specimen of *T. (T.) cricki*, rather than of the other congeneric, but stratigraphically lower, group. Unfortunately there is no definite solution to this problem, as the lectotype of *T. (T.) punctum* is virtually uninterpretable.

The only other species of *Trilobiticer*, *T. (T.) trilobitoides* Buckman and *T. (T.) platygaster* Buckman, both have considerably more coronate inner whorls, a stronger

contraction of the body chamber, and more prominent spines and tubercles. The primary rib density of these two species is also consistently lower at fourteen to eighteen per whorl (average fifteen). As noticed by Crick (1894, p. 436), there is a considerable resemblance between some specimens of *T. (T.) cricki* and members of the *Pseudotoites* group, particularly *P. (Latotoites) evolutum* (Tornquist), (Westermann 1964, pl. 9, fig. 5). Whilst this resemblance could be nothing but another example of convergent evolution and homeomorphy, taking their relative stratigraphic positions into account, it is possible that these antipodean forms evolved from the *Trilobiticerat*/*Emileites* group at the base of the *laeviuscula* Zone.

PHYLOGENETIC SIGNIFICANCE OF NEW TAXA

One of the main requirements for establishing a phylogenetic relationship is a detailed stratigraphic knowledge of the groups concerned. There have been considerable problems in the past in the interpretation of the early history and evolution of the ammonite family Otoitidae. This has largely been due to the inadequate and often erroneous stratigraphic information available to fill the apparent gap between the first well-documented faunas of the *discites* Zone and the diverse and abundant forms of the *sauzei* Zone. One obvious source of confusion has been the error introduced by Mascke (1907) and perpetuated by Westermann (1954); that is, the artificial stratigraphic separation of the microconch *Otoites* above its macroconch counterpart *Emileia*. The other major stratigraphic error which has compounded the difficulties inherent in interpreting the early history of the Otoitids, has centred on the correlation of the horizons now included within the *laeviuscula* Zone. Buckman (1909–1930), when describing several new otoitid species from these horizons, referred them to more than six different hemerae (approximately equal to subzone in present use). When these hemerae were subsequently replaced by Oppel's reinstated *sowerbyi* Zone (Spath 1936), there was little or no evidence available on the correct stratigraphic age of Buckman's taxa. This is particularly true of the faunas ascribed to the 'so-called' *trigonalis* subzone, which were an artificial combination of species from at least two separate horizons (see Parsons 1974, pp. 162–164, 171, for further details). Because of this confusion it has in the past proved impossible to subdivide the highly diverse otoitid faunas found below the *sauzei* Zone (Arkell 1956, p. 33). This unfortunately led Westermann (1964, text-fig. 14) to use dominantly morphological rather than stratigraphic criteria to establish his otoitid phylogeny.

Recent work has revealed that there are numerous inconsistencies present in Westermann's phylogenetic scheme. Groups such as *Labyrinthoceras* and *Frogdenites*, which were linked as macroconch and microconch are now known to occupy different stratigraphic horizons in the *sauzei* and *laeviuscula* Zones respectively, whilst other groups, such as *E. crater*, *E. catamorpha*, *E. brocchii*, and *E. (Otoites) delicata*, which were separated by Westermann, are now known to occur together in the lower part of the 'fossil-bed', Sandford Lane, near Sherborne, Dorset (Parsons 1974, p. 168). It has now proved possible to determine the correct stratigraphic position of most members of the Otoitinae, an essential step prior to establishing

any phylogenetic relationships. The successive otoitid faunas from southern England (after Parsons 1974, pp. 164–171, with additions), are as follows:

(i) *concaum* Zone, rare specimens of *Trilobiticerat* (*T.*) '*punctum*', and its undescribed macroconch, *T. (Emileites)* sp. nov., both of which are morphologically very similar to the *Abbasites* group from the subjacent horizons.

(ii) *discites* Zone, rare specimens of *T. (T.) trilobitoides*, *T. (T.) platygaster* and two undescribed macroconchs, *T. (Emileites)* spp. nov., along with extremely rare specimens of *T. (T.) cricki* nov.

(iii) *ovalis* Subzone, relatively common specimens of *T. (T.) cricki* nov., *T. (E.) malenotatus*, *E. (E.) subcadiconica*, and *E. (Otoites) douvillei* nov.

(iv) *laeviuscula* Subzone (lower part), a diverse fauna of *E. (E.) brocchii*, *E. (E.) catamorphat* Buckman, *E. (E.) contrahens* Buckman, *E. (E.) crater* Buckman, *E. (E.) polyschides* (Waagen), *E. (Otoites) delicata* (Buckman), *E. (O.) douvillei* nov., *E. (O.) sauzei* (d'Orbigny) group, *T. (T.) cricki* nov., and *T. (Emileites)* sp.

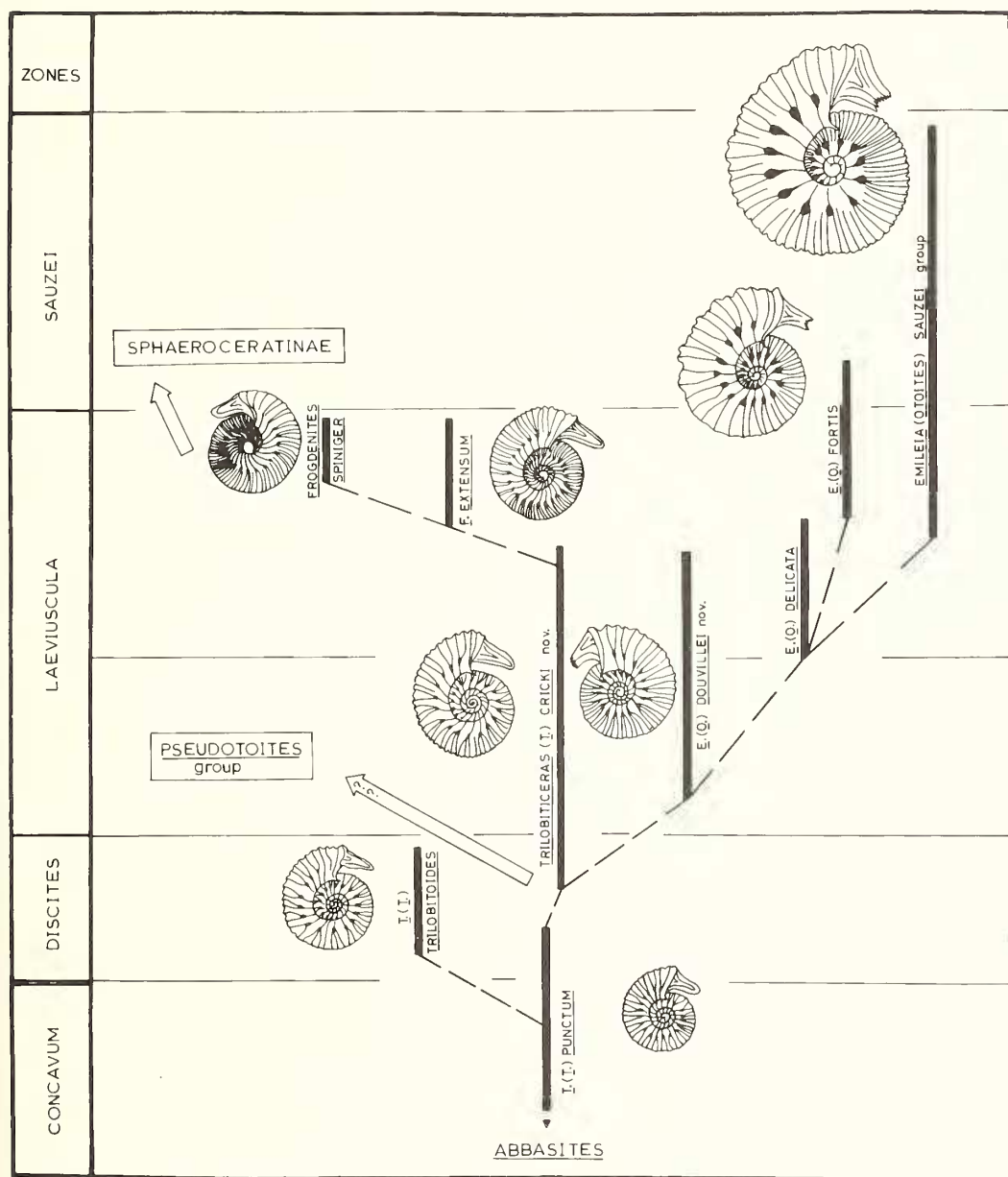
(v) *laeviuscula* Subzone (upper part), *E. (E.) brocchii*, *E. (E.) bulligera* (Buckman), *E. (E.) polyschides*, *E. (Otoites) fortis* (Westermann), *E. (O.) sauzei* group, *Frogdenites extensum* (Buckman), *F. gibberulum* (Buckman), and *F. spiniger* Buckman.

(vi) *sauzei* Zone, *E. (E.) bulligera*, *E. (E.) greppini* Maubeuge, *E. (E.) multifida* Buckman, *E. (E.) polyschides*, *E. (E.) pseudocontrahens* Maubeuge, *E. (Otoites) sauzei* group, and *E. (O.) contracta* (Buckman non Sowerby).

In most of the above faunas, mainly due to lack of material, it is still difficult to specifically link micro- and macroconchs. Thus, except in the case of *Frogdenites*, where the dimorphism is manifestly intraspecific in character, in the bulk of the Otoitinae, following Callomon (1963), dimorphism is best expressed at the sub-generic level. Since morphological diversity is lower in the microconch groups, it is easier to establish a phylogenetic link between their successive populations. A summary of the stratigraphic distribution and probable phylogeny of the main microconch members of the Otoitinae is thus shown in text-fig. 3.

It is clear from this figure that the two new species are of critical phylogenetic importance. *E. (O.) douvillei* is the earliest member of its subgenus and its close relationship with *T. (T.) cricki* finally establishes the *Emileia/Otoites* group as an offshoot of *Trilobiticerat*. *T. (T.) cricki* is of fundamental importance, as it proves to be the root-stock for several important otoitid groups, as well as a long-ranging taxon useful for demonstrating the continuity between the faunas of the *discites* and *laeviuscula* Zones.

The genus *Frogdenites* closely resembles *T. (T.) cricki*, whilst its early members, such as *F. extensum*, also have an overlapping stratigraphic range: both *F. extensum* and *T. (T.) cricki* occur abundantly together in the middle *laeviuscula* Zone of Cape Mondego, Portugal (pers. obs.; Ruget-Perrot 1961, p. 27, bed 5). Specimens of *F. extensum* from north Dorset ('green-grained marl', Osborne Wood, Parsons 1974, p. 167), exhibit relatively coronate inner whorls, with a rapid uncoiling of the umbilical seam, in a similar fashion to *T. (T.) cricki*, to give a more planulate overall shell form. Only the relatively late forms, such as *F. spiniger*, have developed the



TEXT-FIG. 3. The stratigraphic distribution and probable phylogenetic relationship of the main microconch members of the ammonite subfamily Otoitinae in southern England.

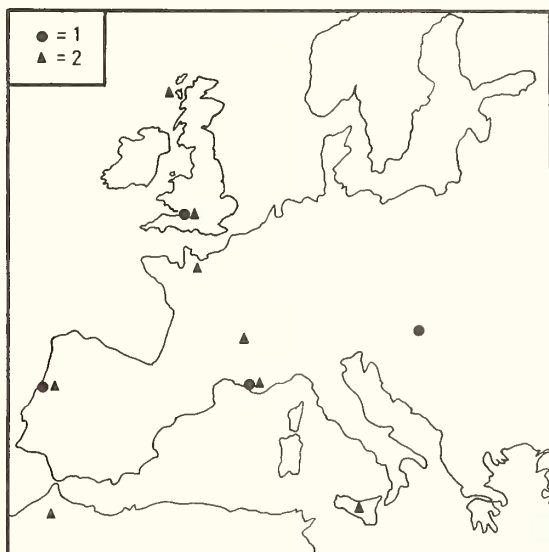
more inflated, involute, sphaeroconic form, which is transitional to the Sphaeroceratinae. *T. (T.) cricki* thus shows both a similar shell form, with coronate inner whorls and fine sharp tubercles, and a similar style of dimorphism, with a low size ratio between dimorphs, to that exhibited by *Frogdenites*. Since *T. (T.) cricki* is the only group to show these characters, which has a contiguous stratigraphic range with *Frogdenites*, it thus forms a highly probable ancestor for the latter genus.

The connection between the *Pseudotoites* group and *T. (T.) cricki* is the most tenuous of the three phylogenetic relationships suggested. *Pseudotoites*, particularly in Western Australia, is cryptogenic, as it appears suddenly in a geographically and stratigraphically isolated horizon, the Newmarracarra Limestone (Arkell and Playford 1954). The only way to determine the origins of such a group is to attempt to establish its relative stratigraphic position, and its similarities and affinities, if any, with possible related groups. The genus *Fontannesia* is abundant in Western Australia, where it forms a monospecific swarm at the base of the Newmarracarra Limestone (ibid., text-fig. 2). *Fontannesia* is found dominantly in the *discites* Zone in Europe, although it possibly ranges up into the base of the *laeviuscula* Zone (Pavia and Sturani 1968, p. 311). It is significant that this genus has been found in New Guinea associated with '*Docidoceras*' *longalvum* (Vacek), another *discites* Zone form (Westermann and Getty 1970). This would suggest that the succeeding *Pseudotoites* fauna (Arkell and Playford 1954, text-fig. 2), is just post-*discites* Zone in age. Since both *Fontannesia* and *Docidoceras* are predominantly Tethyan in origin (Arkell 1956, pp. 177 and 209; Westermann and Getty 1970, p. 291), it is logical to seek the ancestors of the *Pseudotoites* group in the Otoitids of the Tethyan *discites* Zone.

The *Pseudotoites* group shows a high degree of morphological diversity. The Australian macroconchs (*Pseudotoites s. str.*), are medium-sized, relatively inflated forms, with inner whorls exhibiting numerous, fine prorsiradiate secondary ribs (Arkell and Playford 1954, pl. 32, fig. 3), very similar to the *T. (E.) malenotatus* figured here (Pl. 17, fig. 10). The outer whorls show a modified ornament, with the development of short, inflated, nodate primary ribs. This is a similar trend to that shown by some undescribed specimens of *Emileia* from the lowest *laeviuscula* sub-zone at Dundry. The corresponding microconchs (*Pseudotoites (Latotoites)* spp.), included by Arkell in *Otoites* are similar to the latter genus in ribbing style, but differ by being much more evolute. They are thus similar in many characters, except size, to *T. (T.) cricki* nov. There are rare specimens in the Australian faunas which show a close similarity with members of the *T. (T.) trilobitoides* Buckman group: *P. (Latotoites) depressus* (Whitehouse), (Arkell and Playford 1954, pl. 30, fig. 7). Arkell was hesitant about including the latter taxon in *Trilobiticer* because of its greater size (c. 4.0 cm), compared to the much smaller European *Trilobiticer* known at that time. The description of *T. (T.) cricki*, with a maximum diameter in excess of 3.1 cm has thus removed one serious objection to any comparisons between these groups.

On both general morphological and stratigraphic grounds, there is thus no really plausible existing alternative to accepting the *Trilobiticer*/*T. (Emileites)* group as the root stock of *Pseudotoites*. If *Pseudotoites* did not evolve directly from the *T. (T.) cricki* group, then they both must have had a common ancestor in the *discites* Zone. An interesting problem is presented by the relationship of the above groups to the genus *Docidoceras*. As pointed out by Arkell (Arkell and Playford 1954, p. 572), the

type species of this genus, *D. cylindroides* S. Buckman, bears a close morphological relationship to some members of the *Pseudotoites* group. The former species is in fact atypical of the rest of the forms included in *Docidoceras* by Buckman (1909–1930) (Arkell and Playford 1954, p. 572). There is thus a possibility that this species may have had a common origin, with *Trilobiticeras*/*Emileites*, in the *concauum* Zone *Abbasites*, a suggestion already made by Westermann (1969, pp. 129 and 137). The bulk of the other 'species' of '*Docidoceras*', with their more typically stephanoceratid ribbing style, are undoubtedly closely related to some as yet undescribed species, akin to '*D. longalvum*' (Vacek), from the middle *murchisonae* Zone of south Dorset (Senior *et al.* 1970—*Docidoceras* sp., Horn Park quarry, bed 5a). The genus *Docidoceras*, as at present defined, could thus be polyphyletic. It seems certain that *Docidoceras*, taking into account its stratigraphic range and gross morphology, makes a poor dimorphic partner for *Trilobiticeras*; on these grounds *Emileites* is far more satisfactory.



TEXT-FIG. 4. The geographic distribution of 1, *Trilobiticeras* (*Trilobiticeras*) *cricki* sp. nov., and 2, *Emileia* (*Otoites*) *douvillei* sp. nov.

STRATIGRAPHIC SIGNIFICANCE

The two species described here jointly have a restricted stratigraphic range (text-fig. 3) and a wide geographic distribution (text-fig. 4). They thus form an important part of an ammonite fauna, which over most of Europe is characteristic of the basal *ovalis* subzone of the *laeviuscula* Zone (Parsons 1974). Whilst the constituent members of this fauna remain much the same, their relative proportions vary according to geographic position. In southern England, a fairly typical fauna from Barns Batch Spinney, Dundry, has the following proportions: *Witchellia* 46 specimens, *Sonninia* 10, *Trilobiticeras* 17, *Emileia* 2, *Docidoceras* 1, *Bradfordia* 6, *Strigoceras* 2.

To the north in Skye (Inner Hebrides, Scotland), the Sonninidae are almost totally dominant, as apart from an isolated specimen of *E. (O.)* cf. *douvillei* nov., only specimens of *Sommnia s. lat.* and *Witchellia* have been recorded (pers. obs.; Morton 1975). South towards Tethys the Sonninidae become progressively less abundant as there is an increase in diversity linked with a levelling out of the relative proportions of the different ammonite groups present. On the whole in Tethyan and adjoining regions, the Stephanoceratacea and Haploceratacea are the more important. Of these, the genus *Bradfordia* is particularly characteristic of the Lower Bajocian in Bulgaria (Sapunov 1971), Sicily (Renz 1925), and Portugal (pers. obs.). The major exception to this trend appears to be south Germany, where probably due to palaeogeographic isolation, the faunas are largely restricted to *Sommnia s. str.* The most important areas of preservation of *ovalis* subzone faunas in Europe are to be found in England, France, and Germany.

Southern England

The best exposures of rocks assigned to this subzone in England are to be found on Dundry Hill, near Bristol. Here sections at Castle Farm (Buckman and Wilson 1896, p. 676), Barns Batch Spinney (ibid., p. 689), South Main-road (ibid., p. 691), and Rackledown (ibid., p. 692), have all yielded abundant *ovalis* subzone faunas. The most extensive collection from this horizon (the 'Lower white iron-shot'), has been made at Barns Batch Spinney (ibid., p. 689, bed 2), and this includes: *Witchellia (Witchellia) albida* (S. Buckman); *W. (W.) romanoidea* (Douvill ); *W. (W.)* cf. *connata* (S. Buckman); *W. (W.)* cf. *sutneri* (Branco); *W. (Pelekodites) pelekus* (S. Buckman); *W. (P.)* cf. *macra* (S. Buckman); *Sommnia ovalis* (S. Buckman ex Quenstedt); *Euhoplloceras* sp.; *Bradfordia* cf. *inclusa* S. Buckman; *Strigoceras compressum* (S. Buckman); *Toxamblyites* sp.; *Docidoceras* cf. *cylindroides* S. Buckman; *Trilobiticeras (T.) cricki* nov.; *T. (Emileites) malenotatus* (S. Buckman)–*T. (E.) liebi* (Maubeuge) group; *Emileia (Otoites) douvillei* nov.

Other areas in England which have produced similar faunas include the Cotswold Hills (Buckman 1895, p. 397, beds 4–5); the Cole 'syncline', Bruton, Somerset (Richardson 1916, p. 495, bed 6); the Sherborne district, Dorset (Buckman 1893, p. 493, bed 8), and Seavington-St.-Mary, Somerset (Parsons and Torrens *in* Torrens 1969, p. A27, bed 4b).

France

The so-called '*Witchellia*-beds' of Normandy have produced a fauna of at least the *ovalis* subzone (Haug 1893; Bigot 1900; Gabilly and Rioult 1974). The most famous exposures of rocks of this age are, however, to be found to the south near Toulon (Douvill  1885). Here a thin, condensed limestone has produced one of the most diverse faunas from this subzone, which has been described in detail (ibid.). Whilst the stratigraphy and distribution of this bed is well known (ibid.; Lanquine 1929), the interpretation of its fauna has been difficult, as only a few specimens have been figured by modern methods (Lanquine 1929, pls. IX and X). For the rest only the rather stylized drawings provided by Douvill  (1885, pls. I–III) have been available. However, Douvill 's specimens are still preserved in the  cole des Mines Collections, now held at the Universit  de Paris-Sud. The latter has kindly provided

me with photographs of this material, which have enabled a more accurate interpretation of Douvillé's figures to be made:

Plate I, figure 1, *Euhoploceras* sp. 2, ?*E.* sp. 3 and 3a, *E.* sp. 4, *E.* cf. *palnata* S. Buckman. 5, *Witchellia* (*Pelekodites*) cf. *zurcheri* (Douvillé). 6, *W.* (*P.*) *zurcheri*, lectotype, designated by Buckman (1909–1930, pl. 399). 7, *W.* (*P.*) *zurcheri*. 8, *Zurcheria ubaldi* Douvillé.

Plate II, figure 1, *Witchellia* (*Witchellia*) *sayni* Haug. 2–5, *W.* (*W.*) spp.

Plate III, figures 1–2, *W.* (*W.*) sp. 3 and 3a, *W.* (*W.*) *romanoides* (Douvillé). 4, *W.* (*W.*) *romanoides*. 5, *W.* (*W.*) *romanoides*. 6 and 6a, *Bradfordia praeradiata* (Douvillé), lectotype, designated by Sapunov (1971, p. 79). 7, *Bradfordia* cf. *praeradiata*. 8, *Emileia* (*Enileia*) aff. *subcadiconica* S. Buckman. 9, *E.* (*Otoites*) *douvillei* nov. 10, *Trilobiticerias* (*Trilobiticerias*) *cricki* nov.

The two other specimens, which have been figured from this horizon by Lanquine (1929), are *Emileia* (*Otoites*) cf. *douvillei* nov. (ibid., pl. IX, fig. 6) and *Trilobiticerias* (*Emileites*) sp. (ibid., pl. X, fig. 2). This fauna, apart from its slightly higher apparent diversity, is identical to that recorded from Dundry Hill, England; the close similarity of the *Witchellia* groups is particularly striking.

Germany and Switzerland

The Schwabian Albe of south-west Germany and the adjoining Swiss Jura both possess fossiliferous representatives of the *ovalis* Subzone. The 'Unterer Wedelsandstein' of Schwabia (Parsons 1974, p. 173) is the source of the type specimen of *Somminia ovalis* (Buckman ex Quenstedt), and this species is by far the most abundant in these beds. Other less-common forms include rare specimens of *Witchellia* spp. and a solitary specimen of *T. (E.) liebi* (Maubeuge) (Bayer 1968; Parsons 1974, p. 175). The equivalent beds in the Swiss Jura have apparently yielded the type specimens of *T. (E.) liebi* (Maubeuge 1955, pl. 9, figs. 1a–d and 2), but this needs to be confirmed by the collection of *in situ* topotypes.

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